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perspectives for investigating chimpanzee behavior**

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Kristian J. Carlson

Muscle architecture of the common chimpanzee (*Pan troglodytes*): perspectives for investigating chimpanzee behavior

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Abstract Thorpe et al. (Am J Phys Anthropol 110:179–199, 1999) quantified chimpanzee (*Pan troglodytes*) muscle architecture and joint moment arms to determine whether they functionally compensated for structural differences between chimpanzees and humans. They observed enough distinction to conclude that musculo-skeletal properties were not compensatory and suggested that chimpanzees and humans do not exhibit dynamically similar movements. These investigators based their assessment on unilateral limb musculatures from three male chimpanzees, of which they called one non-adult representative. Factors such as age, sex, and behavioral lateralization may be responsible for variation in chimpanzee muscle architecture, but this is presently unknown. While the full extent of variation in chimpanzee muscle architecture due to such factors cannot be evaluated with data presently available, the present study expands the chimpanzee dataset and provides a preliminary glimpse of the potential relevance of these factors. Thirty-seven forelimb and 36 hind limb muscles were assessed in two chimpanzee cadavers: one unilaterally (right limbs), and one bilaterally. Mass, fiber length, and physiological cross-sectional area (PCSA) are reported for individual muscles and muscle groups. The musculature of an adult female is more similar in architectural patterns to a young male chimpanzee than to humans, particularly when comparing muscle groups. Age- and sex-related intraspecific differences do not obscure chimpanzee-human interspecific differences. Side asymmetry in one chimpanzee, despite consistent forelimb directional asymmetry, also does not exceed the

magnitude of chimpanzee-human differences. Left forelimb muscles, on average, usually had higher masses and longer fiber lengths than right, while right forelimb muscles, on average, usually had greater PCSAs than left. Most muscle groups from the left forelimb exhibited greater masses than right groups, but group asymmetry was significant only for the manual digital muscles. The hind limb exhibited less asymmetry than the forelimb in most comparisons. Examination of additional chimpanzees would clarify the full range of inter- and intra-individual variation.

Keywords Muscle mass · Fiber length · Physiological cross-sectional area · Functional anatomy · Bilateral asymmetry

Introduction

Alexander (1974) proposed that muscle properties should reflect the most strenuous activities in which they function. Subsequently, it has become clear that muscle anatomy, including architectural properties, is highly plastic during the lifetime of an individual (Lieber and Fridén 2000, 2001). Striated muscle architecture describes “the arrangement of muscle fibers within a muscle relative to the axis of force generation” (Lieber and Fridén 2000). A muscle usually is optimized for shortening velocity or force production [fiber length or physiological cross-sectional area (PCSA), respectively], neither of which are quantified exclusively by muscle mass (Wickiewicz et al. 1983, 1984; Zajac 1992).

Methods for quantifying muscle architecture were developed from several pioneering studies (e.g., Gans and Bock 1965; Sacks and Roy 1982; Gans and De Vries 1987). Since the length of a sarcomere, which is the unit of contraction in striated muscle, is considered evolutionarily conservative among vertebrates (see Cutts 1988b; Lieber and Fridén 2001), a given fiber length contains an estimable number of sarcomeres in *serial* arrangement (Gans 1982; Schmidt-Nielsen 1990). When

K. J. Carlson
Department of Anatomical Sciences, School of Medicine,
Health Sciences Center, Stony Brook University,
Stony Brook, NY 11794-8081, USA

Present address: K. J. Carlson (✉)
Anthropologisches Institut und Museum, Universität Zürich,
Winterthurerstrasse 190, 8057 Zürich, Switzerland
E-mail: carlson@aim.unizh.ch
Tel.: +41-44-6355415
Fax: +41-44-6356804

the biochemical properties of two muscles are equivalent (i.e., similar fiber-type compositions), the maximum shortening velocity at the muscle tendon will be higher in the muscle with more sarcomeres in series as opposed to the muscle with fewer sarcomeres in series (Sacks and Roy 1982). The PCSA, on the other hand, measures the number of sarcomeres in *parallel* arrangement (Gans 1982; Schmidt-Nielsen 1990). A muscle with greater PCSA theoretically would exert more force when characteristics such as fiber type are equal (Sacks and Roy 1982). When fibers are misaligned with the axis of muscular tendon action, such as occurs in pennated muscles, the effectiveness of a muscle declines (Gans 1982; Sacks and Roy 1982). The incorporation of pennation angle into calculations of muscle PCSA may provide more realistic estimates of muscle performance, but PCSAs remain reasonably accurate when pennation angles below 30° are disregarded (see Gans 1982; Thorpe et al. 1999).

Several primate studies have investigated the relationship between muscle fiber architecture and limb use during locomotor behaviors (Anapol and Jungers 1986; Babcock 1994; Anapol and Barry 1996; Demes et al. 1998; Shahnoor and Anapol 1998; Thorpe et al. 1999; Anapol and Gray 2003), but relatively few data on ape muscle architecture have been reported. In fact, Thorpe et al. (1999) provide the only comprehensive quantification of chimpanzee (*Pan troglodytes*) forelimb and hind limb architectural properties. While these researchers evaluated three individuals (all male) ranging in age from 6 years to adulthood, they reported data from only the 6-year-old chimpanzee because it was “representative” of their sample (Thorpe et al. 1999, p 185). The 6-year-old chimpanzee was compared to adult humans in order to evaluate “... whether chimpanzees have muscle dimensions that allow them to move in a dynamically similar manner to humans ...” through compensation for skeletal differences between the two groups (Thorpe et al. 1999, 179).

Architectural properties have been shown to decline with age in humans matched for height, body mass, and physical activity (Narici et al. 2003). Whether chimpanzees exhibit a similar physiological response, however, is unknown. Young chimpanzees are known to exhibit different locomotor behavior repertoires than adult chimpanzees. Juvenile chimpanzees have been observed to perform more climbing, suspensory behavior, and bipedalism, while adults performed more quadrupedalism (Doran 1992, 1997). Given the plasticity of muscle architecture, behavioral differences between young and adult chimpanzees are suggestive of variable architectural properties whether or not an age-related physiological effect is present.

In addition to age-related effects, sex could be relevant when muscle architectural properties are compared. With respect to percentage of overall locomotion, chimpanzees did not differ significantly based on sex, but there were sexual differences in their percentage of arboreal locomotion (Doran 1993). Male and female

chimpanzees also exhibited dissimilar frequencies of individual arboreal locomotor behaviors (Doran 1993). Sex-specific trends in locomotor repertoires of free-ranging chimpanzees suggest caution is warranted when comparing activity-sensitive muscle architectural properties across sexes.

Behavioral lateralization is yet another possible factor that could influence muscle architectural properties. Activities during which lateralization is expressed in humans, such as handedness, are usually found to accentuate underlying directional asymmetry in limb skeletal dimensions (Pande and Singh 1971; Garn et al. 1976; Pfeiffer 1980; Plato et al. 1980; Haapasalo et al. 2000). The dominant limb was favored relative to the non-dominant limb, especially in the upper limbs. Such lateralization in activity patterns is known to lateralize muscle volume in humans (Chhibber and Singh 1970, 1972; Schell et al. 1985; Maughan et al. 1986; Martorell et al. 1988; Taaffe et al. 1994). The effects of behavioral lateralization on chimpanzee muscle architecture, however, remain to be investigated.

This study has three goals: (1) to broaden the scope of chimpanzee limb muscle architectural properties by providing comprehensive data from two adults, including the first comprehensive data from a female; (2) to compare magnitudes of potential inter- and intra-individual differences with the magnitude of distinction between chimpanzee and human muscle architectures (cf., Thorpe et al. 1999); (3) to comment on chimpanzee intra-individual difference in limb muscle architecture (i.e., bilateral asymmetry). Since the sample is small, comparisons should be viewed as tentative until larger samples of chimpanzee muscle architectural properties are available.

Methods

Two adult common chimpanzees (*Pan troglodytes*) were acquired by the Indiana University Zooarchaeology Laboratory (Table 1). Individual 1 (Ind. 1) was obtained from an unrecorded donor, while individual 2 (Ind. 2) was obtained from the Yerkes Primate Research Center. Background information was available for Ind. 2 only. Individual 2 eventually died of pneumonia and chronic kidney disease, losing approximately 9.6% of her body weight during the 2.5 months preceding her death (H. McClure, personal communication). It is uncertain how much of this weight loss was muscle mass. The enclosure of Ind. 2 restricted her running to short distances, but allowed her to freely perform other locomotor behaviors including climbing. Neither specimen exhibited outward signs of asymmetric muscle wasting, pathological conditions, or traumatic injury. Each specimen was autopsied and fixed by submersion in a formalin-based solution of unknown concentration before being obtained (W. Adams, personal communication). Thus, measurements could not be collected on fresh/frozen tissues. Specimens were stored in a walk-in

Table 1 Specimen background information^a

	Individual 1	Individual 2
Sex	Unknown ^d	Female
Weight at death	Unknown	54.7 kg
Age at death (years)	Unknown	48
Cause of death	Unknown	Pneumonia and chronic kidney disease
Femoral bicondylar length (mm)	–	298.5 (298.0)
Tibial length ^b (mm)	–	247.0 (247.0)
Humeral length ^c (mm)	–	291.0 (285.5)
Radial length (mm)	–	288.5 (285.5)

^aLinear measurements are from left elements, with right element lengths reported in parentheses

^bMaximum length (Bass 1995)

^cSimilar to mechanical length (Carlson 2005)

^dLikely to be a male as assessed by partial remnants of soft tissue. Element lengths are unavailable due to curatorial issues

freezer at -12.2°C until dissection, at which point they were removed and thawed at room temperature. Since muscles that crossed the shoulder and hip joints of Ind. 1 were damaged during autopsy, and since Ind. 1 lacked background information, this specimen was dissected first in order to facilitate a more thorough bilateral dissection of Ind. 2. During dissection, muscles were partitioned when possible such that individual heads were measured separately (e.g., long and short heads of biceps brachii, long and short heads of biceps femoris, lateral and medial heads of gastrocnemius). Bilateral data were collected only from Ind. 2.

Muscle masses were measured in a manner similar to that described by Rauwerdink (1993). Muscle bellies and tendons were separated at the belly-tendon junction, with additional tissues (e.g., epimysium, vascular, or nervous) conservatively removed. Muscles were air-dried until mass-constant. All dry masses were measured in a single day, after which muscles were submerged in a plastic bin filled with water maintained at room temperature. Once the muscles were rehydrated, wet masses were quantified. All wet masses were collected in a single day, after which the muscles were allowed to dry again in open air. This cycle was repeated three times. Since rehydration times could not be standardized satisfactorily, only a single set of wet masses was used. The average of the dry mass measurements for a muscle was compared to its wet mass in order to assess whether the single set of wet mass measurements was representative (Table 2). Wet rather than dry muscle masses were preferred in comparisons with data reported by Thorpe et al. (1999) since their data were derived from fresh/frozen tissues. All masses were recorded with an American Scientific Products model 1200P scale (American Scientific LLC, Columbus, Ohio).

Table 2 Associations between dry and wet limb mass

	r_s	n
Left forelimb average dry versus wet	0.997*	36
Right forelimb average dry versus wet	0.992*	37
Left hind limb average dry versus wet	0.992*	38
Right hind limb average dry versus wet	0.998*	38

*Significant at the $p < 0.01$ level

Fiber length was estimated by measuring bundles of muscle fibers – for example, fascicles (see Thorpe et al. 1999). Since this necessitated the removal of fiber bundles from a muscle, length measurements were taken after the completion of all mass measurements. As many as three non-adjacent fiber bundles per muscle were randomly chosen and removed from a rehydrated muscle. Once a fiber bundle was removed, it was positioned on a flat surface and measured without stretching. Fiber bundle length and fiber length are used interchangeably in the remaining text unless noted.

The ratio obtained by dividing muscle lengths by sarcomere lengths standardizes muscles exhibiting different contraction states. Unfortunately, sarcomere lengths could not be quantified in the present study. Contralateral limb joints, however, were reasonably symmetrical in their degrees of abduction and adduction, extension and flexion, protraction and retraction, and rotation. Shrinkage does not distort muscle lengths in preserved tissues relative to muscle lengths in fresh tissues, as long as the muscles are preserved with intact skeletal attachments (Cutts 1988a). Since this was the case for both Ind. 1 and Ind. 2, their fiber length data should be comparable to data reported by Thorpe et al. (1999).

The physiological cross-sectional area (A) of muscles was calculated following Eq. 1, where m = muscle mass, ρ = muscle tissue density [1060 kg/m^3 (Méndez and Keys 1960)], and l = muscle fascicle length. Fixation of a muscle decreases its PCSA by approximately one-half relative to its PCSA in a fresh state (Kawakami et al. 1994). The two specimens used in this study were assumed to have directly comparable PCSAs, while their PCSAs were assumed to be equivalent to PCSAs reported by Thorpe et al. (1999) when they were half the magnitude.

$$A = m / ((\rho)(l)). \quad (1)$$

Pinnation angles were estimated for several muscles after the completion of the mass measurements. The angle of a majority of fibers in a muscle belly was measured to within 5° using a standard translucent protractor placed on top of the muscle. To maximize

comparability with the chimpanzee and human PCSA data reported by Thorpe et al. (1999), pinnation angles were excluded from all PCSA calculations (see Eq. 1).

As well as reporting properties for individual forelimb (Table 3) and hind limb muscles (Table 4), commonly used functional groups of muscles were compared (Alexander 1974, 1981; Thorpe et al. 1999). Masses and PCSAs for muscle groups were compiled by summing constituent muscles, while group fiber lengths were calculated as weighted harmonic means.

Intra-individual differences (e.g., bilateral asymmetry) were assessed statistically in Ind. 2, but inter-individual differences were assessed only qualitatively. Qualitative comparisons of muscle architecture between different individuals necessitated scaling muscle properties to body size. Muscle properties for Ind. 2 were scaled to a hypothetical body mass of 50 kg for comparison to data reported by Thorpe et al. (1999). Properties within limbs occasionally departed from normal distributions according to one-sample Kolmogorov-Smirnov tests. Data were not transformed, however, since this would have complicated direct comparisons with the data reported by Thorpe et al. (1999). Rather, the non-parametric Wilcoxon signed ranked test was chosen to statistically evaluate intra-individual variation within Ind. 2. The significance level for statistical testing was $p < 0.05$.

Results

Properties for individual muscles are reported as raw values. As the average dry and wet muscle masses are correlated significantly for Ind. 2 ($r_s \geq 0.992$; Table 2), it is reasonable to suggest that single wet mass measurements accurately reflect patterns in mass to the same extent as the averaged dry mass measurements. Muscle properties for the left and right forelimbs are reported in Tables 5 and 6, respectively, while muscle properties for

the left and right hind limbs are reported in Tables 7 and 8, respectively. Results from the Wilcoxon signed ranked tests are reported in the text for assessments of overall limb musculatures, but they are reported for group comparisons only when the results are significant.

Forelimb intraindividual difference

Average muscle mass in the left forelimb is 1.848 or 2.383 g greater than average muscle mass in the right forelimb for dry or wet masses, respectively (Tables 5, 6). The side difference in muscle mass is significant whether dry ($n = 36$, $Z = -2.285$, $p = 0.022$) or wet ($n = 36$, $Z = -2.089$, $p = 0.037$) masses are considered. Average fiber length in the left forelimb is greater than in the right forelimb by 6.01 mm (Tables 5, 6), but this difference is not significant ($n = 36$, $Z = -1.076$, $p = 0.282$). Average PCSA in the right forelimb exceeds average PCSA in the left forelimb by 0.467 or 1.029 cm² for dry or wet PCSA, respectively (Tables 5, 6). The side difference in PCSA is not significant whether dry ($n = 35$, $Z = -0.131$, $p = 0.896$) or wet ($n = 35$, $Z = -0.491$, $p = 0.623$) PCSAs are considered.

Forelimb interindividual difference

Architectural properties for muscle groups of Ind. 2 are reported in Table 9. The masses of left forelimb groups are frequently less than one-half the masses of Chimp 95 groups and consistently less than the masses of human groups reported by Thorpe et al. (1999) (Table 10). Individual 2 and Chimp 95, however, exhibit a pattern more similar to each other than to humans when ranking group masses (Table 11).

Forelimb groups of Ind. 2 and Chimp 95 are relatively similar in average fiber length and average PCSA. They exhibit more similarity in average fiber length than average mass when comparing the absolute difference

Table 3 Forelimb muscle groups

Muscle group ^a	Muscles
Wrist flexors	Flexor carpi ulnaris, flexor carpi radialis, flexor digitorum superficialis, and flexor digitorum profundus
Wrist extensors	Extensor carpi ulnaris, extensor carpi radialis brevis, extensor carpi radialis longus, and extensor digitorum
Elbow flexors	Biceps brachii, brachialis, and brachioradialis
Elbow extensors	Triceps brachii
Digital muscles	Flexor digitorum superficialis, flexor digitorum profundus, extensor digitorum, extensor digiti minimi, and extensor indicis
Pollical muscles	Flexor pollicis longus, abductor pollicis longus, extensor pollicis longus, and extensor pollicis brevis

^aExcept for digital and pollical groups, functional groupings are the same as those of Thorpe et al. (1999)

Table 4 Hind limb muscle groups

Muscle group ^a	Muscles
Quadriceps	Rectus femoris, vastus lateralis, vastus medialis, and vastus intermedius
Adductors	Adductor magnus, adductor brevis, and adductor longus
Hamstrings	Semimembranosus, semitendinosus, biceps femoris (longum only), and gracilis
Plantar flexors	Gastrocnemius, soleus, and plantaris
Deep hind flexors	Flexor hallucis longus and flexor digitorum longus
Digital muscles	Extensor digitorum longus and flexor digitorum longus
Hallucal muscles	Extensor hallucis longus and flexor hallucis longus

^aExcept for digital and hallucal groups, functional groupings are the same as those of Thorpe et al. (1999)

Table 5 Left forelimb muscle properties

Muscle (left)	Ind. 2 dry mass ^a (g)	Ind. 2 wet mass (g)	Ind. 2 fiber length ^b (mm)	Ind. 2 pinnation angle ^c (°)	Ind. 2 dry PCSA (cm ²)	Ind. 2 wet PCSA (cm ²)
Trapezius	71.9	149.2	79		8.6	17.9
Rhomboideus	24.8	45.3	104		2.2	4.1
Levator scapulae	6.6	13.0	95		0.7	1.3
Deltoides	84.7	172.7	94		8.5	17.4
Supraspinatus	19.7	38.2	20		9.1	17.7
Infraspinatus	34.6	74.2	42	15	7.8	16.7
Teres major	58.1	115.4	130		4.2	8.4
Teres minor	7.0	14.0	46		1.4	2.9
Subscapularis	48.5	94.7	63	10	7.3	14.2
Latissimus dorsi	167.2	266.9	255		6.2	9.9
Serratus anterior	83.1	136.3	102		7.7	12.6
Dorsoepitrochlearis	8.4	14.7	114		0.7	1.2
Pectoralis major	x ^d	x	208		x	x
Pectoralis minor	9.5	17.1	75		1.2	2.1
Coracobrachialis	12.2	23.7	58	15	2.0	3.8
Triceps brachii	95.0	188.1	85	10	10.5	20.9
Biceps brachii (longum)	15.7	30.2	122		1.2	2.3
Biceps brachii (mediale)	31.7	62.9	158		1.9	3.8
Brachialis	45.3	83.9	125		3.4	6.3
Brachioradialis	22.8	42.6	158		1.4	2.5
Aconeus	3.0	5.7	38		0.7	1.4
Extensor carpi radialis longus	7.3	13.8	87		0.8	1.5
Extensor carpi radialis brevis	7.5	15.5	x		x	x
Extensor digitorum	13.5	26.6	87		1.5	2.9
Extensor digiti minimi	2.1	4.5	70	5	0.3	0.6
Extensor carpi ulnaris	6.5	11.5	65	15	0.9	1.7
Abductor pollicis longus	10.0 ^e	17.0 ^e	35	25	2.7 ^e	4.6 ^e
Extensor pollicis brevis	x	x	x		x	x
Extensor indicis	1.0	1.8	45		0.2	0.4
Extensor pollicis longus	1.9	3.3	45	10	0.4	0.7
Supinator	9.8	20.4	25		3.6	7.6
Pronator teres	9.7	19.3	35	15	2.6	5.2
Pronator quadratus	2.9	5.0	25		1.1	1.9
Flexor carpi radialis	15.2	27.7	60	15	2.4	4.4
Palmaris longus	NP ^f	NP	NP		NP	NP
Flexor carpi ulnaris	16.8	30.3	50	20	3.1	5.7
Flexor digitorum superficialis	32.5	66.0	55	20	5.6	11.3
Flexor digitorum profundus	30.2	64.1	73		3.9	8.2
Flexor pollicis longus	7.9	15.7	60	25	1.3	2.5

^aThe average of at least three measurements per muscle^bThe average of three fiber bundles lengths chosen from random locations within a muscle^cEstimated when possible^dAn “x” denotes a measurement was excluded due to post-mortem damage^eIncluded extensor pollicis brevis^fAn “NP” denotes a muscle that was not present in the individual

between chimpanzees as a percentage of the absolute magnitude in Chimp 95 (Table 10). The group pattern in rankings of average fiber lengths for Ind. 2 is similar not only to Chimp 95, but also to the human pattern reported by Thorpe et al. (1999) (Table 11). Multiple forelimb muscle groups of Ind. 2 exhibit average PCSAs that are approximately half the size of Chimp 95 average PCSAs reported by Thorpe et al. (1999) (Table 10). Since PCSAs derived from fresh and preserved tissues differed by a factor of two due solely to tissue treatment (Kawakami et al. 1994), Ind. 2 and Chimp 95 have relatively equivalent PCSAs, especially in comparison to the human pattern reported by Thorpe et al. (Table 11).

Muscle groups exhibit consistent side differences in Ind. 2, but these are rarely significant (Table 12). Left groups are regularly larger in muscle mass and average

fiber lengths than right groups. The only statistically significant asymmetry is in wet mass of the manual digital group ($n = 5$, $Z = -2.023$, $p = 0.043$). Since most muscle groups contain less than five individual muscles, however, statistical significance is limited by small samples. It is worth noting that muscles in several groups are consistent in directional asymmetry, even though side asymmetry in contralateral groups was non-significant (Tables 5, 6, 7, 8).

Hind limb intraindividual difference

Average dry muscle mass in the left hind limb is 0.14 g greater than in the right (Tables 7, 8), but this side difference is not significant ($n = 38$, $Z = -0.950$, $p = 0.342$).

Table 6 Right forelimb muscle properties

Muscle (right)	Ind. 1 dry mass (g)	Ind. 2 dry mass ^a (g)	Ind. 1 wet mass (g)	Ind. 2 wet mass (g)	Ind. 2 fiber length ^b (mm)	Ind. 2 pinnation angle ^c (°)	Ind. 2 dry PCSA (cm ²)	Ind. 2 wet PCSA (cm ²)
Trapezius		64.1		132.1	64		9.4	19.5
Rhomboideus	35.9	26.2	78.7	52.8	126		2.0	3.9
Levator scapulae		5.9		10.7	106		0.5	0.9
Deltoides	105.3	95.2	272.9	194.3	x		x	x
Supraspinatus		19.6		39.5	27		7.0	14.0
Infraspinatus		36.2		73.7	40	20	8.5	17.2
Teres major	52.1	29.3	123.7	53.0	123		2.2	4.1
Teres minor	8.5	6.5	19.9	11.6	58		1.0	1.9
Subscapularis		45.9		88.6	49	15	8.8	16.9
Latissimus dorsi	132	169.3	326.7	308.4	275		5.8	10.6
Serratus anterior		70.7		126.0	91		7.3	13.0
Dorsoepitrochlearis	20.0	8.7	48.6	15.5	120		0.7	1.2
Pectoralis major	112.8	x ^d	260.2	x	135		x	x
Pectoralis minor	11.2	8.5	24.4	14.9	97		0.8	1.5
Coracobrachialis	15.1	9.0	37.1	16.9	26	40	3.2	6.1
Triceps brachii	186.2	90.2	469.2	170.7	82	10	10.4	19.7
Biceps brachii (longum)	30.2	18.1	75.5	34.7	88		2.0	3.7
Biceps brachii (mediale)	48.8	25.7	119.6	52.4	115		2.1	4.3
Brachialis	48.9	43.7	139.7	86.3	88		4.7	9.2
Brachioradialis	37.0	21.0	101.0	38.3	158		1.3	2.3
Aconeus	3.1	3.0	8.6	5.7	40		0.7	1.4
Extensor carpi radialis longus	16.2	7.6	39.8	13.6	91		0.8	1.4
Extensor carpi radialis brevis	15.7	8.0	39.3	15.7	56	10	1.3	2.6
Extensor digitorum	21.0	12.1	50.5	24.7	89		1.3	2.6
Extensor digiti minimi		2.4		4.2	70	10	0.3	0.6
Extensor carpi ulnaris		5.6		10.7	62	15	0.8	1.6
Abductor pollicis longus	9.0	8.2 ^e	21.6	14.9 ^e	28	25	2.8 ^e	5.0 ^e
Extensor pollicis brevis	4.4	x	10.9	x	x		x	x
Extensor indicis	3.0	0.8	6.8	1.6	52		0.2	0.3
Extensor pollicis longus		1.8		3.4	68	10	0.2	0.5
Supinator		10.0		22.7	24		3.9	8.8
Pronator teres	16.8	7.9	42.5	15.9	48	15	1.6	3.1
Pronator quadratus		2.6		4.4	24		1.0	1.8
Flexor carpi radialis	23.6	13.2	58.1	24.6	48	15	2.6	4.8
Palmaris longus		0.8		1.4	36		0.2	0.4
Flexor carpi ulnaris	19.3	9.5	54.8	19.9	41	25	2.2	4.6
Flexor digitorum superficialis		31.9		64.4	47	15	6.4	13.0
Flexor digitorum profundus	54.4	31.7	142.0	62.3	71		4.2	8.3
Flexor pollicis longus		7.9		16.4	67	20	1.1	2.3

^aThe average of at least three measurements per muscle^bThe average of three fiber bundles lengths chosen from random locations within a muscle^cEstimated when possible^dAn “x” denotes a measurement was excluded due to post-mortem damage^eIncluded extensor pollicis brevis

Average wet muscle mass in the right hind limb is 0.582 g greater than in the left (Tables 7, 8), but the side difference is again non-significant ($n=38$, $Z=-0.339$, $p=0.734$). Contrasting directional asymmetry in average dry and wet muscle mass of the hind limbs suggests that the level of muscle mass asymmetry in Ind. 2 is trivial. Average fiber length in the right hind limb is 1.23 mm greater than in the left hind limb (Tables 7, 8), but the side difference is not significant ($n=34$, $Z=-1.300$, $p=0.194$). The magnitude of hind limb asymmetry in average fiber length is smaller than is exhibited in the forelimbs. Average PCSA in the left hind limb is 0.385 or 0.672 cm² greater than in the right hind limb for dry or wet PCSAs, respectively (Tables 7, 8), but the side difference is significant for neither dry ($n=34$, $Z=-1.547$, $p=0.122$) nor wet PCSA ($n=34$, $Z=-1.274$, $p=0.203$).

Hind limb interindividual difference

Muscle group properties for the hind limb are reported in Table 9. Groups from the left hind limb of Ind. 2 frequently exhibit less than one-half the mass of comparable groups in Chimp 95 (Table 10) and are consistently below values for human groups reported by Thorpe et al. (1999). Individual 2 and Chimp 95 have generally similar patterns in muscle masses when relative group sizes are compared (i.e., mass rankings), although they differ in ranked positions of the adductor and quadriceps groups (Table 11).

All muscle groups of Ind. 2 exhibit shorter average fiber lengths than those reported for Chimp 95 (Thorpe et al. 1999), sometimes disproportionately so (e.g., adductors, hamstrings, plantar flexors, and

Table 7 Left hind limb muscle properties

Muscle (left)	Ind. 2 dry mass ^a (g)	Ind. 2 wet mass (g)	Ind. 2 fiber length ^b (mm)	Ind. 2 pinnation angle ^c (°)	Ind. 2 dry PCSA (cm ²)	Ind. 2 wet PCSA (cm ²)
Tensor fasciae latae	3.3	5.3	96		0.3	0.5
Sartorius	19.9	33.9	300		0.6	1.1
Vastus lateralis	53.5	116.5	63	10	8.0	17.4
Rectus femoris	28.4	53.4	73	10	3.7	6.9
Vastus medialis	37.2	73.6	54	15	6.5	12.8
Vastus intermedius	49.7	110.4	63		7.4	16.5
Iliopsoas	92.0	151.9	107 ^d		8.1	13.4
Iliacus			92			
Psoas			122			
Pectineus	6.0	10.1	77		0.7	1.2
Gracilis	41.0	70.2	249		1.6	2.7
Adductor magnus (medius)	72.0	135.8	121		5.6	10.6
Adductor magnus (caudalis)	111.1	193.9	139		7.5	13.1
Adductor longus	17.2	28.9	107		1.5	2.5
Adductor brevis	12.0	21.1	84		1.3	2.4
Semimembranosus	27.5	48.1	63	20	4.1	7.2
Semitendinosus	37.0	64.3	86		4.0	7.0
Biceps femoris (longum)	28.1	49.0	49		5.4	9.4
Biceps femoris (breve)	15.2	28.1	74		2.0	3.6
Gluteus maximus	123.5	212.9	49		23.6	40.7
Gluteus medius	113.3	206.0	50	25	21.5	39.1
Gluteus minimus	8.8	15.1	46		1.8	3.1
Piriformis	7.9	12.7	33	30	2.3	3.7
Gemellus superior	5.8	10.5	38		1.5	2.6
Obturator internus	13.8	22.6	21	35	6.1	10.0
Gemellus inferior	1.3	2.4	19		0.6	1.2
Obturator externus	14.9	26.1	50		2.8	5.0
Quadratus femoris	9.1	16.8	39		2.2	4.1
Gastrocnemius (lateralis)	15.1	27.6	46	20	3.1	5.6
Gastrocnemius (medius)	26.5	48.4	41	15	6.0	11.0
Soleus	41.6	79.4	23	35	16.8	32.1
Plantaris						
Popliteus	8.8	16.3	38		2.2	4.0
Peroneus longus	14.7	29.2	51		2.7	5.4
Peroneus brevis	6.9	11.9	48	15	1.4	2.4
Tibialis anterior	27.2	59.2	83		3.1	6.8
Tibialis posterior	14.1	29.5	25	25	5.3	11.1
Flexor digitorum longus	7.5	14.2	50	20	1.4	2.7
Extensor digitorum longus	8.9	17.2	109	10	0.8	1.5
Flexor hallucis longus	17.9	30.1	67		2.5	4.2
Extensor hallucis longus	2.9	4.9	83		0.3	0.6

^aThe average of at least three measurements per muscle^bThe average of three fiber bundle lengths chosen from random locations within a muscle^cEstimated when possible^dThe average of six fiber bundle length measurements – three from iliacus and three from psoas

quadriceps) (Table 10). Muscle groups generally display the same patterns (i.e., length rankings) in Ind. 2 and Chimp 95, especially relative to the human pattern reported by Thorpe et al. (1999) (Table 11). Hind limb similarity between Ind. 2 and Chimp 95 is less obvious than forelimb similarity, particularly because of the disproportionately shorter quadriceps and plantar flexors of Ind. 2.

Average PCSAs of the hind limb groups in Ind. 2 are infrequently one-half the average of PCSAs in the Chimp 95 groups reported by Thorpe et al. (1999) (Table 10). Individual 2 and Chimp 95 exhibit broadly similar values for average PCSA of adductors, hamstrings, plantar flexors, and quadriceps. Deep hind flexors, pedal digital, and hallucal groups of Ind. 2, on

the other hand, have average PCSAs well below one-half the values exhibited by the Chimp 95 groups reported by Thorpe et al. (1999). Despite differing in age and sex, however, Ind. 2 and Chimp 95 exhibit similar patterns in PCSA rankings when compared to the human pattern reported by Thorpe et al. (1999) (Table 11).

Magnitudes of hind limb group asymmetry in muscle mass or PCSA tend to exceed magnitudes of asymmetry in forelimb groups, despite the absence of significant side asymmetries in the hind limb (Table 10). Side differences in hind limb muscle groups are less consistent in direction compared to forelimb muscle groups (Table 12). While magnitudes of hind limb group asymmetry in muscle mass or PCSA tend to exceed magnitudes of asymmetry in forelimb groups, the inconsistent

Table 8 Right hind limb muscle properties

Muscle (right)	Ind. 1 dry mass (g)	Ind. 2 dry mass ^a (g)	Ind. 1 wet mass (g)	Ind. 2 wet mass (g)	Ind. 2 fiber length ^b (mm)	Ind. 2 pinnation angle ^c (°)	Ind. 2 dry PCSA (cm ²)	Ind. 2 wet PCSA (cm ²)
Tensor fasciae latae	7.2	3.4	17.3	5.9	108		0.3	0.5
Sartorius	31.9	19.5	69.2	34.1	289		0.6	1.1
Vastus lateralis	111.0	70.1	288.1	158.7	70	15	9.4	21.4
Rectus femoris	43.4	28.4	99.6	53.2	79	10	3.4	6.4
Vastus medialis	52.6	35.0	128.2	69.5	59	15	5.6	11.2
Vastus intermedius	72.8	30.3	187.2	62.0	71		4.0	8.2
Iliopsoas		88.7		152.7	x ^d		x	x
Iliacus					x			
Psoas					x			
Pectineus	7.8	5.2	19.3	8.6	71		0.7	1.1
Gracilis	64.9	46.6	145.3	84.6	233		1.9	3.4
Adductor magnus (medius)	96.0	74.5	231.8	131.8	117		6.0	10.7
Adductor magnus (caudalis)	70.7	120.7	170.6	216.7	141		8.1	14.5
Adductor longus	54.7	18.4	126.0	32.3	111		1.6	2.7
Adductor brevis		13.0		23.7	87		1.4	2.6
Semimembranosus	14.8	25.5	35.0	48.7	62	15	3.9	7.4
Semitendinosus	71.6	46.8	181.5	94.4	x		x	x
Biceps femoris (longum)	26.1	29.7	61.8	49.2	64		4.4	7.3
Biceps femoris (breve)	26.6	14.6	66.2	28.4	88		1.6	3.0
Gluteus maximus	99.2	123.2	249.1	231.6	61		19.1	35.8
Gluteus medius	130.4	108.6	314.1	197.0	48		21.2	38.5
Gluteus minimus	22.3	12.2	54.4	21.4	44		2.6	4.6
Piriformis		11.3		18.8	36	30	3.0	5.0
Gemellus superior	0.9	3.3	1.9	6.0	18		1.7	3.1
Obturator internus		12.1		21.1	18	30	6.2	10.9
Gemellus inferior		1.3		2.4	x		x	x
Obturator externus		13.7		24.1	52		2.5	4.4
Quadratus femoris	6.0	8.2	14.0	15.6	38		2.1	3.9
Gastrocnemius (lateralis)	21.0	12.4	50.0	23.0	46	15	2.5	4.7
Gastrocnemius (medius)	35.8	24.9	89.0	45.3	42	20	5.5	10.1
Soleus	68.2	33.8	164.9	61.2	25	40	12.7	23.1
Plantaris	2.8		6.1					
Popliteus	9.0	7.3	22.4	14.3	37		1.9	3.6
Peroneus longus	19.7	12.6	46.3	22.3	x		x	x
Peroneus brevis	9.2	5.4	21.8	9.2	52	20	1.0	1.7
Tibialis anterior	36.9	24.2	80.7	46.3	80		2.8	5.5
Tibialis posterior	23.4	12.6	58.4	24.1	24	25	5.0	9.5
Flexor digitorum longus	13.6	7.9	29.3	14.4	50	15	1.5	2.7
Extensor digitorum longus	14.5	9.5	31.2	17.7	119	5	0.8	1.4
Flexor hallucis longus	29.2	18.5	74.3	34.2	63	15	2.8	5.1
Extensor hallucis longus	7.4	3.0	15.9	5.1	88		0.3	0.5

^aThe average of at least three measurements per muscle^bThe average of three fiber bundle lengths chosen from random locations within a muscle^cEstimated when possible^dAn “x” denotes a measurement was excluded due to post-mortem damage

directional asymmetry likely explains the lack of significant differences in overall hind limb musculature.

Discussion

It was not surprising that PCSAs of the female adult (Ind. 2) on occasion could differ from one-half the values of non-adult PCSAs (Chimp 95), which is the expected equivalency value for preserved and fresh/frozen tissues (Kawakami et al. 1994). In other words, chimpanzees of different ages can vary in PCSA magnitudes. Age has been shown to affect muscle architectural properties in height, weight, and activity level-matched humans (Narici et al. 2003). It is important to note,

however, that while Ind. 2 and Chimp 95 differed in the magnitudes of adjusted properties, chimpanzees of different ages retained similar *patterns* when relative comparisons of muscle groups within an individual were made.

The comparison of Ind. 1 and Ind. 2 suggested a sex difference, but a larger sample of chimpanzee muscle architectural properties would be necessary for more definitive confirmation. As with age-related differences in muscle architectural properties, the amount of the sex-related difference (e.g., Ind. 1 versus Ind. 2) did not obscure previously reported chimpanzee-human distinctions (Thorpe et al. 1999). Age- and sex-related differences in mass, fiber length, and PCSA tended to exceed the magnitude of side difference observed in

Table 9 Muscle properties for functional groups

	Muscle mass (g)						Ind. 2 fiber length (cm)		Ind. 2 PCSA (cm ²)			
	Dry			Wet					Dry		Wet	
	Ind. 2 left	Ind. 2 right	Ind. 1 ^a	Ind. 2 left	Ind. 2 right	Ind. 1 ^a	left	right	left	right	left	right
Elbow flexors	115.5	108.5	164.9	219.6	211.7	435.8	13.8	10.2	7.9	10.1	14.9	19.5
Elbow extensors	95.0	90.2	186.2	188.1	170.7	469.2	8.5	8.2	10.5	10.4	20.9	19.7
Wrist flexors	94.7	86.3	(97.3) ^c	188.1	171.2	(254.9) ^c	6.0	5.3	15.0	15.4	29.6	30.7
Wrist extensors	34.8	33.3	(52.9) ^d	67.4	64.7	(129.6) ^d	8.1 ^e	7.4	(3.2) ^d	4.2	(6.1) ^d	8.2
Manual digital	79.3	78.9	(78.4) ^f	163.0	157.2	(199.3) ^f	6.6	6.0	11.5	12.4	23.4	24.8
Pollical	19.8	17.9	(9.0) ^g	36.0	34.7	(21.6) ^g	4.4	4.2	4.4	4.1	7.8	7.8
Quadriceps	168.8	163.8	279.8	353.9	343.4	703.1	6.2	6.9	25.6	22.4	53.6	47.2
Adductors	212.3	226.6	(221.4) ^h	379.7	404.5	(528.4) ^h	12.5	12.5	15.9	17.1	28.6	30.5
Hamstrings	133.6	148.6	177.4	231.6	276.9	423.6	8.3	9.5 ⁱ	15.2	(10.2) ⁱ	26.4	(18.1) ⁱ
Plantar flexors ^b	83.2	71.1	127.8	155.4	129.5	310.0	3.0	3.2	25.9	20.7	48.7	37.9
Deep flexors	25.4	26.4	42.8	44.3	48.6	103.6	6.0	5.8	3.9	4.3	6.9	7.8
Pedal digital	16.4	17.4	28.1	31.4	32.1	60.5	7.1	7.3	2.2	2.3	4.2	4.1
Hallucal	20.8	21.5	36.6	35.0	39.3	90.2	6.9	6.5	2.8	3.1	4.8	5.6

^aRight limbs only^bExcluded plantaris^cExcluded flexor digitorum superficialis^dExcluded extensor carpi ulnaris^eExcluded extensor carpi radialis brevis^fExcluded flexor digitorum superficialis^gExcluded extensor pollicis longus and flexor pollicis longus^hExcluded adductor brevisⁱExcluded semitendinosus

Ind. 2 when most muscle groups were considered. The magnitudes of these muscle architectural differences were tempered somewhat by the unknown effect of the weight loss on the magnitudes of Ind. 2 properties preceding her death.

A small number of chimpanzees varying in age and sex exhibited a greater similarity in muscle architectural properties amongst themselves than any single individual exhibited with humans. In expressing their desire to

compare “overall designs” of *P. troglodytes* and humans, Thorpe et al. (1999) observed longer fiber lengths in chimpanzees relative to humans after scaling groups of muscles to a hypothetical body mass (50 kg). They attributed this to the requirements of arboreal locomotion, namely that chimpanzees must exert force throughout greater joint excursions compared to humans. Muscle groups of Ind. 2 scaled to a 50-kg body mass usually exhibited greater average fiber lengths than

Table 10 Muscle properties predicted for a hypothetical 50-kg Individual 2^a, Chimp 95^b, and modern human^b

	Wet mass (kg)				Fiber length (cm)				Wet PCSA (cm ²)			
	Left	Asymmetrical	Chimp	95 Human	Left	Asymmetrical	Chimp	95 Human	Left	Asymmetrical	Chimp	95 Human
Elbow flexors	0.20	0.01	0.60	0.31	13.39	3.49	13.9	13.8	14.03	−4.33	40.6	21.4
Elbow extensors	0.17	0.02	0.45	0.33	8.25	0.29	10.4	7.7	19.68	1.13	41.1	40.1
Wrist flexors	0.17	0.02	0.58	0.28	5.82	0.68	9.2	7.1	27.88	−1.04	58.9	37.2
Wrist extensors	0.06	0.00	0.21	0.14	7.86 ^c	—	7.7	5.9	5.75 ^d	—	25.9	21.6
Manual digital	0.15	0.01	0.47 ^c	—	6.41	0.58	10.2 ^c	—	22.04	−1.32	44.5 ^c	—
Pollical	0.03	0.00	0.05 ^d	—	4.27	0.19	4.4 ^d	—	7.35	0.00	11.4 ^d	—
Quadriceps	0.32	0.01	0.74	1.30	6.02	−0.68	10.2	5.7	50.48	6.03	68.4	215.5
Adductors	0.35	−0.02	0.71	0.70	12.13	0.00	22.0	9.2	26.94	−1.79	30.6	72.2
Hamstrings	0.21	−0.04	0.57	0.69	8.06	—	19.6	8.3	24.87	—	27.4	78.2
Plantar flexors	0.14	0.02	0.39	0.63	2.91	−0.19	7.4	2.4	45.87	10.17	49.5	252.3
Deep hind flexors	0.04	0.00	0.16	0.07	5.82	0.19	6.6	2.9	6.50	−0.85	23.5	22.0
Pedal digital	0.03	0.00	0.09	—	6.89	−0.19	7.9	—	3.96	0.09	11.2	—
Hallucal	0.03	0.00	0.12	—	6.70	0.39	7.4	—	4.52	−0.75	16.0	—

^aAsymmetry reported for Ind. 2 only, and was calculated as left minus right such that positive values occurred when left groups were larger and negative values occurred when right groups were larger^bData reported by or calculated from Thorpe et al. (1999)^cExcluded extensor indicis and extensor digiti minimi^dExcluded flexor pollicis longus^eExcluded extensor carpi radialis brevis

Table 11 Ranked muscle groups for scaled muscle properties^a

	Wet mass			Fiber length			Wet PCSA		
	Ind. 2	Chimp 95	Human	Ind. 2	Chimp 95	Human	Ind. 2	Chimp 95	Human
Elbow flexors	1	1	2	1	1	1	3	3	4
Elbow extensors	2.5	3	1	2	2	2	2	2	1
Wrist flexors	2.5	2	3	3	3	3	1	1	2
Wrist extensors	4	4	4	—	4	4	—	4	3
Quadriceps	2	1	1	5	3	3	1	1	2
Adductors	1	2	2	1	1	1	3	3	4
Hamstrings	3	3	3	2	2	2	4	4	3
Plantar flexors	4	4	4	7	5.5	5	2	2	1
Deep hind flexors	5	5	5	6	7	4	5	5	5
Pedal digital	7	7	—	3	4	—	7	7	—
Hallucal	6	6	—	4	5.5	—	6	6	—

^aManual digital and pollical groups are not included in rankings since complete data are unavailable for Chimp 95 and human groups reported in Thorpe et al. (1999). Forelimb and hind limb groups are ranked separately. Forelimb groups are ranked from largest/longest (1) to smallest/shortest (4). Hind limb groups also are ranked from largest/longest (1) to smallest/shortest (7)

Table 12 Direction of asymmetry for muscle groups in Individual 2^a

	Dry mass		Wet mass		Fiber length		Wet PCSA	
	Left	Right	Left	Right	Left	Right	Left	Right
Elbow flexors	←		←		←		→	
Elbow extensors	←		←		←		←	
Wrist flexors	←		←		←		→	
Wrist extensors	←		←		NA		NA	
Manual digital	←		← [*]		←		→	
Pollical	←		←		←		= ^b	
Quadriceps	←		←		→		←	
Adductors	→		→		= ^b		→	
Hamstrings	→		→		NA		NA	
Plantar flexors	←		←		→		←	
Deep hind flexors	→		→		←		→	
Pedal digital	→		→		→		←	
Hallucal	→		→		←		→	

NA missing measurements

^{*}Significant at $p < 0.05$

^aArrows point towards larger/longer side

^bSimilar to one decimal place

human muscle groups reported by Thorpe et al. (1999). Thorpe et al. (1999) went on to suggest that fiber lengths, being more similar between the forelimbs and hind limbs of chimpanzees than they are in humans, reflected the greater equivalency in limb use among chimpanzees, which they attributed to chimpanzees engaging in more quadrupedalism than bipedalism. Individual 2, an adult female, exhibited an even greater similarity between forelimb and hind limb average fiber lengths than those reported for Chimp 95 (Thorpe et al. 1999). While specific details of locomotor behaviors for Ind. 2 were not recorded (e.g., percentages), her enclosure neither restricted quadrupedalism nor prevented arboreal locomotor behaviors.

Bilateral asymmetry (left > right) in overall muscle mass was more prominent in the forelimb of Ind. 2 than in her hind limb. This is potentially interesting given the evidence available for a chimpanzee trend in forelimb behavioral lateralization (Hopkins 1993, 1994, 1995; Morbeck et al. 1994; Colell et al. 1995; Holder 1999;

Lacreuse et al. 1999; Palmer 2002; reviewed in Hopkins and Morris 1993; but see Marchant and McGrew 1996; McGrew and Marchant 1997). Neither humans (Chhibber and Singh 1970; Young et al. 2002) nor chimpanzees have been associated with a limb preference in the hind limbs. Many of the aforementioned chimpanzee behavioral studies investigated forelimb preferences during activities (e.g., food reaching, water drinking, and termite fishing) that seldom involved vigorous physical exertion, and the expression of a limb preference during more physically vigorous locomotor behaviors has not been reported in free-ranging populations (Doran 1989, 1992, 1993, 1996; Doran and Hunt 1994; Hunt 1989, 1991a, b, 1992), despite suggestive skeletal forelimb asymmetry in chimpanzees (left > right; Morbeck et al. 1994). The evidence for chimpanzee forelimb asymmetry, however, is far less persuasive than the human evidence (right > left; Chhibber and Singh 1972; Schell et al. 1985; Maughan et al. 1986; Martorell et al. 1988; Taaffe et al. 1994; Proctor

et al. 2002). Muscle volumes from a large sample of chimpanzees could be obtained through minimally invasive ultrasound or magnetic resonance imaging technologies (e.g., Kawakami et al. 2000) and may be useful in addressing potential behavioral lateralization.

While lateralization in muscle volume has been linked to limb dominance in humans (e.g., Maughan et al. 1986; Taaffe et al. 1994), the extent to which it is observed in muscle architecture has not been addressed. I am aware of only one study that can be used to assess human bilateral asymmetry in muscle architecture. Kawakami et al. (2000) used bed-rest and exercise regimes on five males, ages 20–27. Average muscle volume and PCSA were greater in the pre-exercised right quadriceps femoris muscles, except for vastus lateralis, which was greater in volume only, while average fiber length was greater in the pre-exercised left side. Bilateral asymmetries in chimpanzee average wet mass, average fiber length, and average PCSA (i.e., typically from 5 to 20% of total magnitude) often did not obscure differences in muscle architecture reported in chimpanzee and human muscle groups (Thorpe et al. 1999). Future studies of primate muscle architecture should investigate the possibility of directional asymmetry using larger samples and a wider range of muscles, particularly in the forelimb.

Tendencies to lateralize lead and trail forelimbs (e.g., stride lengths) have been reported in horses (Deuel and Lawrence 1987). Whether chimpanzees also exhibit forelimb lateralization during quadrupedal gaits is unclear. Chimpanzees display the tendency to over stride with their hind limbs during quadrupedalism (Larson and Stern 1987). By angling their trunk away from the median sagittal plane (i.e., deviating the longitudinal axis of their torso to the left or right), they prevent hind limbs from interfering with forelimbs. The shift in trunk angle establishes an outside forelimb (positioned outside the over striding hind limb) and an inside forelimb (positioned inside the over striding hind limb). Larson and Stern (1987) reported that although chimpanzees used either forelimb as the outside limb, one chimpanzee tended to use the left forelimb as an outside limb, while another chimpanzee regularly used the right forelimb as an outside limb. Given the reported differences in muscle activity and shoulder abduction between the outside and inside forelimbs, it is conceivable that muscle architecture could reflect these limb preferences. Whether lateralization in muscle architecture can be linked to lateralization in gait, however, awaits future studies that would correlate muscle architecture (e.g., PCSA), EMG, and kinematic data.

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